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The effect of flow speed and food size on the capture efficiency and feeding behaviour of the cold-water coral *Lophelia pertusa*

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ABSTRACT

The capture efficiency and feeding behaviour of the cold-water coral (CWC) *Lophelia pertusa* (Linnaeus, 1758) were investigated considering: (1) different food types, (2) different food sizes and (3) different current speeds and temperatures. This study used two different multifactorial experimental approaches: (1) Corals were subjected to three different flow speeds (2, 5 and 10 cm s^{-1}) in 5 l volume tanks, and three different food types (alive zooplankton, alive algae, and dry particulate organic carbon) were offered to the corals under each current regime, analysing the capture rates of the corals under these different flow velocities. (2) In a flume, the feeding behaviour of the coral polyps was studied under different current speed regimes (1, 7, 15 and 27 cm s^{-1}) and a temperature change over a range of 8–12 °C. The obtained results confirm that low flow speeds (below 7 cm s^{-1}) appear optimal for a successful prey capture, and temperature did not have an effect on polyp expansion behaviour for *L. pertusa*. In conclusion, flow speeds clearly impact food capture efficiency in *L. pertusa*, with zooplankton predominantly captured prey at low flow velocities (2 cm s^{-1}) and phytoplankton captured at higher flow velocities of 5 cm s^{-1}. This split in capture efficiency may allow corals to exploit different food sources under different tidal and flow conditions.

1. Introduction

Knowledge of the biology and ecology of cold-water corals (CWC) has markedly improved over the last two decades. One of the main focal points of research has been the trophic ecology for some CWC species, principally *Lophelia pertusa*. The works by Tsounis et al. (2010) and Purser et al. (2010) demonstrated that food capture rates and efficiency were largely dependent upon prey size and generally low current velocity in *L. pertusa* (1–2.5 cm s^{-1}).

The exact diet of CWC species has been of debate for many years (e.g. Kiriakoulakis et al., 2005; Duineveld et al., 2004, 2012; Dodds et al., 2009). Carlier et al. (2009) presented the first stable isotope analyses of *L. pertusa* and demonstrated that zooplankton were the most assimilated prey in the tissue of *L. pertusa* collected in Mediterranean waters, but signals of phytoplankton were also detected. Phytoplankton appears to be one of the main food for other cold-water cnidarians, such as several species of Antarctic gorgonian (Elias-Piera et al., 2013). Determining food sources and assimilation rates are important due to the increasing focus on the ecophysiology of CWC, as certain food sources may play important roles in maintaining basic physiological processes, such as respiration and growth in CWC (Naumann et al., 2011).

Under changing environmental conditions in the deep ocean, it is expected that CWC species will need to adapt to different food types and sizes, altered current velocities and temperatures. Some previous

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studies on these topics have been conducted in Mediterranean and Antarctic waters, where the ability of some gorgonian corals to capture different prey types and sizes, as well as particles have been evaluated. Ribes et al. (1998, 1999), and Orejas et al. (2001, 2003) demonstrated that not only zooplankton but also organisms belonging to the "small sized plankton fraction" (e.g. ciliates and flagellates) were actively consumed by octocorals. These small preys, consumed in large amounts, where found supply around 50% of the daily energetic demand of these Antarctic organisms (Orejas et al., 2003), as such the importance of a varied diet cannot be overlooked in CWC.

To date there is no information on the ability of *L. pertusa* in capturing different food types and sizes under different current flow and temperature regimes, nor is there nutritional information in the amount of carbon (C) that different food types can supply. Information is also lacking on the relationship between polyp behaviour and different current and temperature regimes and how this could affect capture efficiency. In this study, the capture efficiency of *L. pertusa* was determined using two different experimental approaches: 1) Three different food types commonly observed in CWC habitat (fresh alive zooplankton, phytoplankton, and particulate organic carbon (POC)) were offered to *L. pertusa* and capture rates calculated under different flow velocities using 5 l cylindrical tanks. 2) *L. pertusa* polyp expansion/retraction behaviour was quantified in a recirculating flume, under different flow velocities and temperatures.

2. Materials and methods

2.1. Coral sampling and hatching

Corals were collected at depths ranging from 123 to 190 m during three different cruises (two in May 2010, one in November 2011) using the RV *Calanus* within the Mingulay Reef area in the Sea of Hebrides (Fig. 1). Samples were collected by means of a small Van Veen grab equipped with a video camera that allowed highly targeted sampling of coral fragments with limited damage to the reef. After collection, corals were transferred to the aquaria facilities at the Scottish Association for Marine Science (SAMS). Specimens were maintained in tanks with re-circulating seawater at 8–9 °C until the experiments were carried out in a temperature-controller room set at 8 °C. A third cruise took place in May–June 2012 on board the RRS *James Cook*, and samples were collected by means of the Irish Holland-1 ROV. Corals were maintained on board in tanks with re-circulating seawater at 8–9 °C until the experiments were carried out on board the research vessel.

2.2. Feeding experiments

Experiments were performed using experimental chambers previously developed by Orejas et al. (2001, 2003) (Fig. 2A). The chambers have a cylindrical shape and 5 l volume. Each chamber is supplied with a motor and a stirrer that keeps the water in movement at flow velocities ranging from 1 to 10 cm s^{-1}. Flow speed was determined using an electromagnetic current metre (AEM1-D, ALEC Electronics, Kobe, Japan). Chambers were filled with 4 l of filtered seawater (0.2 μm), and coral nubbins (two per chamber) were placed into each experimental chamber, while two skeletons of coral were placed into the control chamber. Corals were allowed to acclimate to the experimental conditions for approximately 1–2 h, and experiments started when polyps were fully expanded. Food capture was assessed under three different flow speeds (2, 5 and 10 cm s^{-1}) for six coral nubbins (two per chamber) and two nubbin skeletons in the control chamber (Fig. 3A) for each food type (fresh living zooplankton, diatom algae *Skeletonema marinoi* Sarno and Zingone, 2005, and POC). A total of 14 nubbins were used for the experiments with zooplankton and phytoplankton as food items, and a total of 22 for the experiments with POC. All nubbins had polyps of similar size, and all polyps were alive. The number of polyps per nubbin ranged from 3 to 11 (mean 6 polyps ± 2 SD), and capture rates were standardised to units per polyp.

2.2.1. Food type

The food types presented to *L. pertusa* were based on the opportunistic feeding behaviour displayed by corals, and benthic suspension feeders in general. In particular, zooplankton and phytoplankton were selected as food sources for *L. pertusa* based on observations from previous studies (e.g. Carlier et al., 2009). Fresh living zooplankton were collected in the same day or one day before the experiments, by the RV *Calanus* or the RV *Seol Mara* in the Firth of Lorn (56.469129 °N; 5.4881859 °W) using a 1 m diameter plankton net (mesh size 270 μm) in 30 m vertical hauls. Zooplankton were stored in a cool box until it arrived at the laboratory, where they were kept at 8 °C with slight aeration. These samples were visually examined under a stereo miscroscope, with Copepoda being the most abundant taxon in the zooplankton samples.

The diatom algae *S. marinoi* represented the phytoplankton food source, and were obtained from the Culture Collection of Algae and Protozoa (CCAP, Oban, UK). The strain (CCAP 1077/5) was grown in sterile modified F/2 medium (Guillard and Ryther, 1962; Guillard, 1975). Cultures were maintained at 20 °C under a mixture of cool-white and

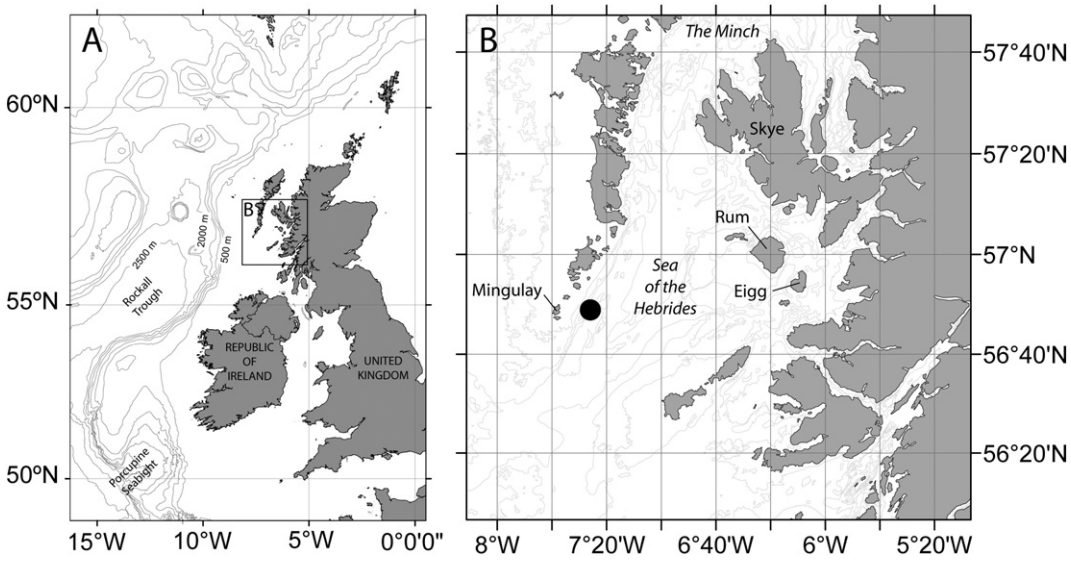

Fig. 1. Map of the sampling location. A: General overview. B: Detail of the location of the Mingulay Reef Complex (black circle).

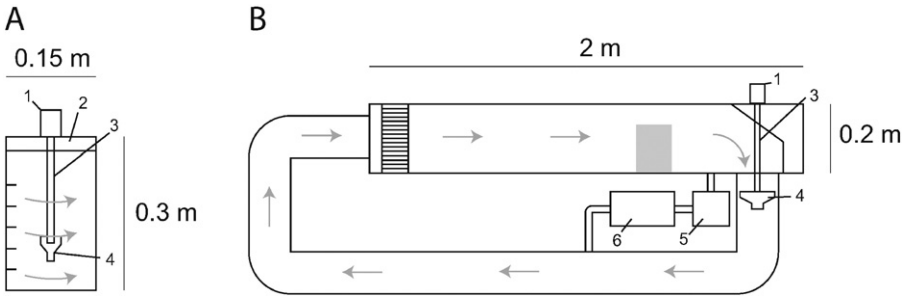

Fig. 2. Design of experimental flumes. A: Closed recirculation system for feeding trials and B: flume for behaviour observations. Grey arrows show water flow direction. 1) 24 V motor, 2) lid, 3) motor shaft, 4) propeller, 5) small pump (2500 L h^{-1}), 6) chiller.

warm-white fluorescent tubes at ~100 μmol photons m^{-2} s^{-1} PAR and a 12 h/12 h light/dark regime. Cultures were periodically sub-cultured by the aseptic transfer of an inoculum (~5% (v/v) of the original culture) to fresh, sterile F/2 medium. *S. marinoi* is one of the main constituents of the phytoplankton community in the Sea of Hebrides, forming important spring blooms (Kooistra et al., 2008). Due to the shallow depths of the Mingulay reefs, it is likely that phytoplankton such as *S. marinoi* could reach the reefs during the regular downwelling events observed and are likely be a potential food source for corals (Davies et al., 2009). Finally, lyophilized powder from cultured algae (*Thalassiosira rotula* Meunier, 1910), provided by Ocean Lab (University of Aberdeen), was used as the particulate organic carbon (POC) source.

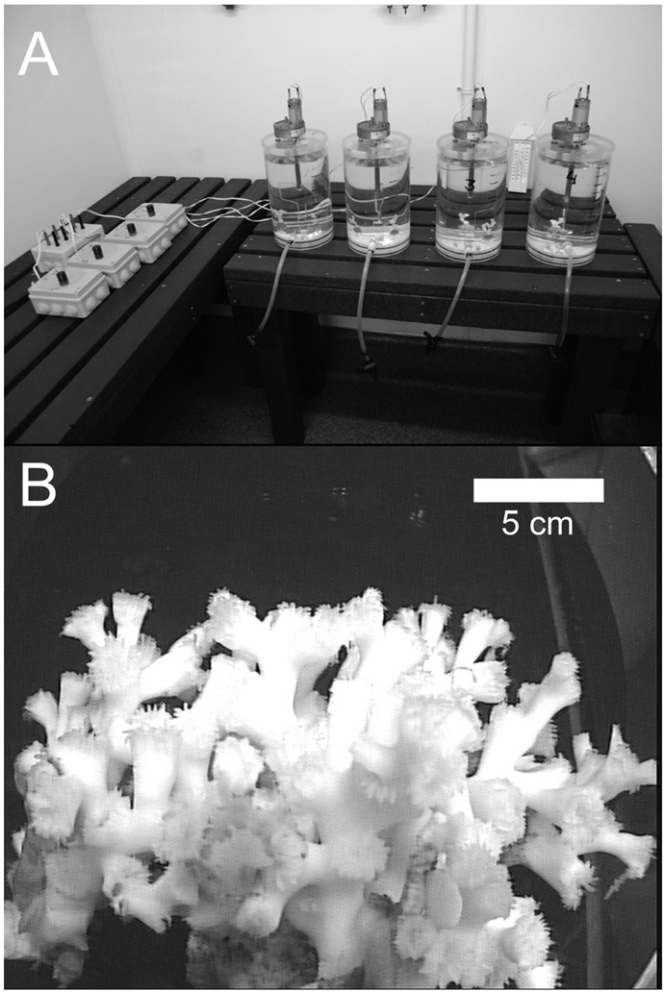

Fig. 3. The experimental set-ups used for the experiments. A: The four chambers used in the feeding experiments (three experimental and one control). In each chamber two coral nubbins were placed. In the left part of the image the controllers that manipulate the speed of the paddles can be seen. B: An example *Lophelia pertusa* coral clump used in the flume experiment, the water flow direction was from the top of the image.

2.2.2. Zooplankton capture rates

The fresh living zooplankton were initially concentrated to ~-40 copepods ml^{-1}, via manual sorting of the sample using a Bogorov plate. In each chamber, 100 ml of this copepod concentrate was added at the beginning of the experiments to reach a starting concentration of approximately 100 copepods l^{-1}. After a couple of seconds (to allow a homogeneous distribution of the zooplankton in the chamber), initial samples (T_0) of 250 ml were taken from each chamber. After four hours of incubation, final samples (T_f) of the same volume were collected from each chamber. All samples were preserved in 4% aqueous formaldehyde for subsequent counting under microscopy by means of a Bogorov plate.

2.2.3. Phytoplankton capture rates

Ten milliliters of *S. marinoi* culture (culture pure concentration around 1,200,000 cells ml^{-1}) was added in each chamber at the beginning of the experiments to reach a starting concentration of approximately 2,993,000 cells l^{-1}. After a couple of seconds (to allow a homogeneous distribution of the phytoplankton in the chamber), initial samples (T_0) of 15 ml were taken from each chamber. After 4 h of incubation, final samples (T_f) of the same volume were collected from each chamber. All the samples were preserved in lugols solution for subsequent counting under microscopy by means of a Sedgewick rafter counting chamber.

2.2.4. Particulate organic carbon capture rates

Five miligrams of a dry extract from the diatom *T. rotula* was added to each chamber at the beginning of the experiments. The 5 mg contained approximately 200 μg of POC. After a couple of seconds (to allow a homogeneous distribution of the powder in the chamber), initial samples (T_0) of 500 ml were taken from each chamber. After 4 h of incubation final samples (T_f) of the same volume were collected from each chamber. Samples from each experiment were filtered through previously combusted (500 °C; 4 h) GF/F filters, stored in cryovials and frozen at −20 °C until analysis.

2.2.5. Carbon analyses

Carbon content of the food items (zooplankton, phytoplankton and POC) was determined in order to estimate the amount of C supplied to the corals by each food type. Three zooplankton subsamples (each containing 200 individuals) and 6 phytoplankton subsamples (3 subsamples of 60 ml with 0.28 cells μl^{-1} and 3 subsamples of 30 ml with 0.41 cells μl^{-1}) were analysed by means of a Costech International Elemental Combustion System (ECS) 4010 using a pneumatic autosampler. Operational temperatures were set to 1000 °C in the left combustion furnace, 650 °C in the right reaction furnace and 50 °C in the gas chromatographic separation oven. The helium (>99.9%) carrier gas pressure was set to 1.2 bar giving a flow rate ~100 ml min^{-1}. Oxygen (>99.9%) used for combustion was set at 1.9 bar and air (water and oil

free) at 2.4 bar. Six standards of acetanilide (BDH Chemicals — 10.36% Nitrogen, 71.09% Carbon) were weighed into the same batch of 5 × 9 mm tin capsules from a range from 0.1 mg to 3.5 mg. The analysis was run for 15 min on the 'Semi-μ' setting. A single capsule of acetanilide per 12 unknown samples, was also weighed. These reference samples were measured as unknown samples to allow any instrument drift to be corrected. Calibration drift over long analytical sessions is small, and typically <2%. The analysis of the C content contained in the algal powder supplied as the third food source was assessed with the previously mentioned pre-combusted GF/F filters. The filters were preserved at −20 °C and elemental analyses of POC were carried in Liverpool John Moores University using an NC 2500 CE CHN analyser following Yamamouro and Kayanne (1995).

2.3. Flume experiments

Experiments were carried out using a recirculating flume constructed following designs by Vogel and LaBarbera (1978) and consisted of a 1.5 m long by 20 cm wide by 20 cm high open channel constructed from acrylic plastic with a PVC return pipe beneath the flume (8 cm diameter) (Fig. 2B). Water flow was generated by a 24 V motor powered by an adjustable bench power supply (Thurlby Thandar Instruments EL303R) and was capable of generating flows of up to 50 cm s^{-1} using a brass propeller housed in the return pipe (Fig. 2B). Flow passed through two collimators with a grid aperture of 1 cm^2 at the beginning and end of the open channel, with flow velocities calibrated using a Nortek Vectrino ADV. The entire flume was housed in an insulated box, with seawater supplied from a nearby aquarium of the same type as in the first experiment. Seawater temperature was maintained at the chosen temperature using an aquarium chiller (Deltec DC300).

Clumps of *L. pertusa* polyps (Fig. 3B) (n = 5 for flow velocity trials and n = 6 for temperature trails) were sensitively placed into the flume and allowed to acclimate during for one hour, prior to starting flow. During the second hour the clumps were introduced to a flow of 0.5 cm s^{-1} ± 0.6 cm s^{-1} and seeded with 1 ml of macerated, concentrated food mixture (5 g *Calanus glacialis* Jaschnov, 1955 ground in 10 ml of seawater) to stimulate polyp expansion. No further food was added to the flume, as the focus in this experiment was on polyp expansion behaviour. Observations were recorded as a 10 s interval time-lapse using a standard definition colour video camera and video recorder.

The binary response of *L. pertusa* (e.g. either retracted or extended) was determined for each observation using an image analysis procedure in the package ImageJ (version 1.47 t) as follows: 1) a 4 × 4-pixel area adjacent to a polyp was marked, usually at the start of observation when nearly all polyps were retracted. Ten polyps in total were selected for each experimental run providing the polyp was clearly observable and in focus, and it extended outwards against a dark background. 2) The state of each polyp then assessed manually using 10 randomly selected frames to validate the procedure. As the polyp changed between states, there was a change in the greyscale value (values ranged between zero = black and 255 = white). When the greyscale values of the extended and contracted phases overlapped, the point where the two states intersected was calculated, providing a point where a polyp was more likely to be in one state or the other. 3) The extracted values were either contracted (0) or extended (1) and were used to track individual polyp response and were converted to a proportion that demonstrated colonial response from the ten observed polyps.

Two experiments were conducted. Firstly, five colonies from independent samples were subjected to four different flow velocities for a duration of 1 h at each speed (0.5 ± 0.6 cm s^{-1}, 6.7 ± 1.5 cm s^{-1}, 15 ± 3 cm s^{-1} and 27 ± 4.7 cm s^{-1}) at a constant seawater temperature (8 °C). Polyp behaviour was assessed after 55 min of exposure to a given flow velocity, as polyps can take approximately 30 min to respond to stimulus (Mortensen et al., 2001). Secondly, in a separate experiment six independent colonies were maintained at 8.5 °C (±0.2 °C) for a 2 h acclimation period. Three were maintained at this temperature for a 4-h period to act as controls and to account for individual colony variability in response. The other three were subjected to a temperature change of 1 °C h^{-1} to a maximum of 12 °C. For analysis purposes, the observation period was split into two temperature ranges: 8–10 °C (first 2 h of observation for controls), and 10–12 °C (final 2 h of observation for controls). Flow velocity was maintained at a constant flow of 0.5 ± 0.6 cm s^{-1}. Polyp behaviour was assessed after 2 h of exposure to a given temperature range to allow time for polyps to respond to the temperature stimulus for recording. These conditions were selected to match general conditions observed at the Mingulay Reef complex (Davies et al., 2009) and differed from feeding trials due to the greater capability of this flume in generating consistent flows.

2.4. Data analysis

Capture rates in the feeding experiments were calculated as the control-corrected decrease in prey or C concentrations throughout the incubation time, normalized to the number of polyps. Polyp behaviour in the flume experiments was treated as a proportional colonial response from ten observed polyps.

Normal distribution of data was tested by means of Kolmogorov–Smirnov tests performed with the R-language function ks.test, and homogeneity of variances was tested by mean of the Bartlett test performed with the R-language function bartlett.test of the R software platform (R Core Team 2014). The effect of flow velocity on capture rates of each food type and the effect of temperature on polyp behaviour was tested by means of the nonparametric Kruskal–Wallis rank sum test performed with the R-language function kruskal.test since some of the data were not normally distributed or variances were not homogeneous. For significant effects, subsequent nonparametric multiple comparison procedure was performed with the R-language function nparcomp which is available in the nparcomp library (Konietschke et al., 2015). The effect of flow velocity on polyp behaviour was tested using one-way repeated measures analysis of variance using the R-language function lme, with proportions arcsine transformed prior to analysis, and assumptions of normality and homogeneity tested as above. For significant effects, subsequent multiple comparisons were conducted using the Tukey HSD multi-comparison test in the R-language function multcomp with Bonferroni corrections.

3. Results

3.1. Capture rates of zooplankton, phytoplankton and POC under different flow speeds

Capture rates changed significantly with flow velocity for zooplankton (Kruskal–Wallis chi-squared = 5.956, p = 0.05) and phytoplankton (Kruskal–Wallis chi-squared = 5.956, p = 0.05), with corals capturing more prey items at 2 and 5 cm s^{-1} than 10 cm s^{-1} (Tukey test, p-value < 0.001) (Fig. 4A and B). POC was not consumed by polyps under any current regime, with concentrations increasing under 5 and 10 cm s^{-1} flow velocities (Fig. 3C). POC values did not change significantly with flow speed (Kruskal–Wallis chi-squared = 0.72, p = 0.698).

The highest C capture by the corals from phytoplankton occurred at 5 cm s^{-1} current (up to 2324.7 μg C h^{-1} $polyp^{-1}$, Table 1), whereas the highest C capture from zooplankton was at 2 cm s^{-1} (250.35 μg C h^{-1} $polyp^{-1}$).

3.2. Feeding behaviour under different flow speeds and temperatures

A change in flow speed resulted in a different proportion of polyps that were expanded (Repeated Measures ANOVA, $F_{3,12}$ = 3.82, p = 0.039) (Fig. 5). Multiple comparisons revealed that more polyps were expanded at 6.7 cm s^{-1} compared to 27.6 cm s^{-1} (Tukey test, p =

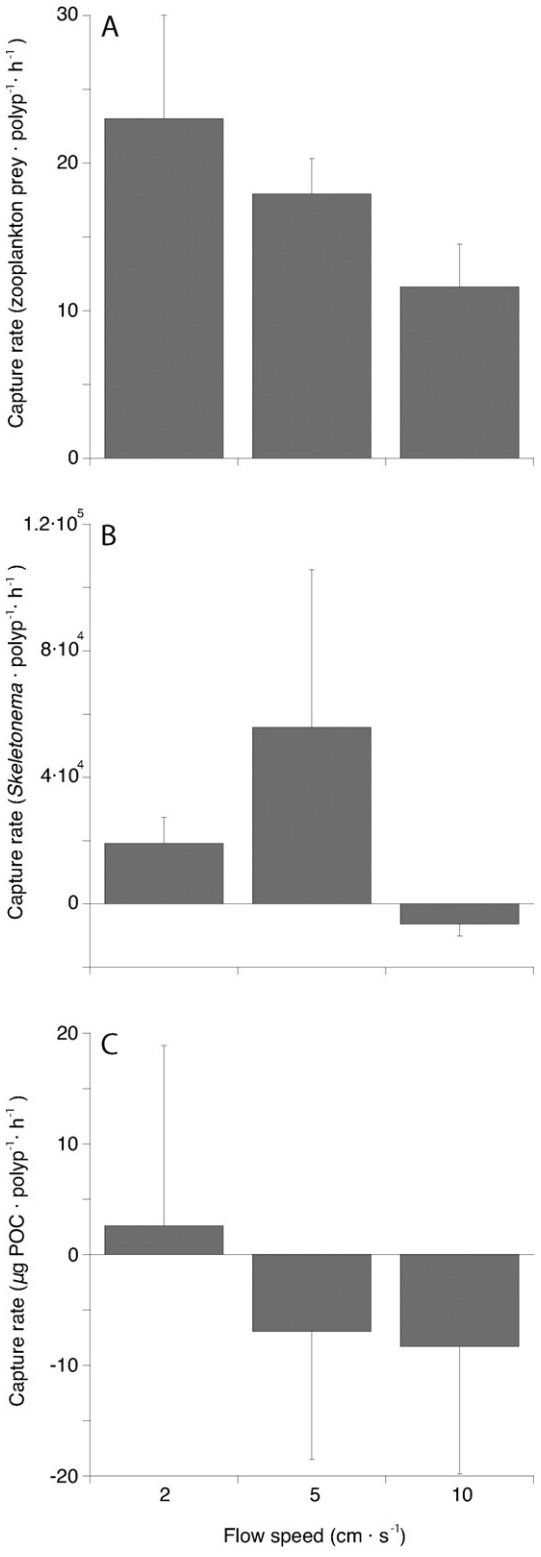

Fig. 4. Capture rates (average ± SD) for *Lophelia pertusa* under three different flow speed (2, 5 and 10 cm/s) for the different prey items. A: Zooplankton capture rate (zooplankton prey per polyp per hour); B: algae capture rate (*Skeletonema* per polyp per hour); C: particulate organic carbon capture rate (µg POC per polyp per hour).

0.017), with no other comparisons being significant. The colony responses for different temperature exposures did not show any significant differences (Kruskal–Wallis chi-squared = 0.05, p = 0.827), nor did the control treatment (Kruskal–Wallis chi-squared = 0.808, p = 0.369) (Fig. 6).

4. Discussion

L. pertusa most efficiently captured the tested food types under low flow speeds (2 and 5 cm s^{-1}), confirming that low current velocities are optimal for feeding in this CWC, as previously documented using *Artemia salina* (nauplii and adults) as prey items (Purser et al., 2010). Whilst 2 cm s^{-1} seems to be the optimal current speed for *L. pertusa* to capture zooplankton (copepods), the diatom *S. marinoi* was captured more efficiently at 5 cm s^{-1}. Polyp expansion behaviour was also greater at low flow speeds (i.e. 0.5 and 6.7 cm s^{-1}) compared to higher velocities (15.1 and 27.6 cm s^{-1}), which corroborates the results of the feeding experiments. These results show that polyps may be stimulated to expand at low rather than at high speeds, potentially due to greater drag on the polyp and a lower probability of particle capture. It is important to stress that the maximum and average net capture rates determined in this study do not necessarily equal the number of items successfully ingested by *L. pertusa*, they rather represent the removal from suspension by direct consumption, entrapment within polyp mucus, or weighting down following contact with polyp-derived mucus.

L. pertusa has been reported as associated with high-energy hydrodynamic environments (Roberts et al., 2009) with high bottom current velocities (e.g. Thiem et al., 2006; White et al., 2007; White and Dorschel, 2010; Khripounoff et al., 2014) and strong flow speed variations (e.g. Davies et al., 2009, 2010; Mienis et al., 2007, 2012). These periods of strong currents are often short and driven by the tide or stochastic events. During most periods, near bottom currents recorded in CWC sites are lower than 15 cm s^{-1} (White and Dorschel, 2010; Mienis et al., 2012; Khripounoff et al., 2014) with average flow speeds between 5 and 15 cm s^{-1} (Duineveld et al., 2007; Mienis et al., 2007, 2009, 2012; Davies et al., 2010). High capture rates under low flow speed are probably widespread within a reef-forming species, especially those that are highly branched, such as *L. pertusa*. Many areas of reduced flow are likely to occur within the rugose structure of a complex three-dimensional reef structure (Purser et al., 2010; also observed in tropical coral reefs see Sebens and Johnson, 1991). We hypothesise that this occurs on a variety of scales, ranging from not only large reef but also smaller colonies and may be an underlying driver for why many suspension feeders occur in dense patches. Colonies of *L. pertusa* probably dissipate higher current velocities with increasing size, potentially explaining why large colonies are capable of surviving at high recorded current velocities (i.e. 60 cm s^{-1} Mienis et al., 2014). In the Mingulay Reef, where the corals used in these experiments were collected, the strong prevailing currents are reduced in velocity for a period of several hours during each tidal cycle, decreasing to less than 2 cm s^{-1} (Davies et al., 2009). Feeding at high currents becomes potentially less effective for *L. pertusa* (Purser et al., 2010). In the flow velocity experiment, it was observed that a greater proportion of polyps were retracted at higher flow velocities suggesting some polyps were not actively feeding. Clearly, at velocities where polyp tentacles are progressively swept back, the feeding surface is greatly reduced (LaBarbera, 1984; Dai and Lin, 1993; Purser et al,. 2010).

Temperature has been observed to fluctuate greatly in the field. For example, the complex hydrodynamic regime of the Mingulay Reef complex (the source of the experimental animals) described by Davies et al. (2009) incorporates both the lateral advection of particles and a tidally controlled rapid down welling that forces warmer waters from the surface (about 0.5–1 °C warmer than average) that have higher concentrations of fluorescent matter. The metabolism of *L. pertusa* increased almost two-fold during temperature increases of 1 °C in the laboratory (Dodds et al., 2007). This suggests that enhanced feeding to counteract higher metabolic rates is required during periods of elevated temperature (i.e. increased temperatures cause starvation if met with insufficient increase in food supply). The results obtained in the flume, regarding different temperature regimes, revealed no significant influence on the proportion of expanded polyps when exposed to a change

Table 1
Average (±SD) carbon content (expressed as microgram per hour and per polyp) supplied by the different prey items (copepods, unicelular alga *Skeletonema marinnoii* and particulate organic carbon (POC)), under the three different current speed used in the feeding experiments.

	Copepods (μg C h^{-1} p^{-1})	Unicelular alga (μg C h^{-1} p^{-1})	POC (μg C h^{-1} p^{-1})
2 cm s^{-1}	250.35 ± 79.45	798.4 ± 343.02	2.60 ± 16.26
5 cm s^{-1}	194.84 ± 26.12	2324.7 ± 2085.00	−8.55 ± 12.57
10 cm s^{-1}	126.26 ± 32.57	−264.3 ± 158.41	−9.65 ± 11.11

of 2–4 °C. However, it should be taken into account that the duration of temperature change was short in order to replicate conditions at Mingulay (Davies et al., 2009), and the detection of any temperature effects on polyp behaviour may need longer experimental periods. In addition, only a binary response of the polyps (i.e. expanded or retracted) was recorded, and did not take into account mucus production or polyp surface area, that are likely to be important in particle capture and more affected by temperature (e.g. Naumann et al., 2010 and references therein). Furthermore, an additional food signal was not added into the flume during the observation periods. As a result, the increased temperature in experimental treatments was not matched with the same food signal as the initial temperature treatment, likely confounding the result of the experiment.

The obtained results stress the importance of phytoplankton as a food source for CWC, which may profit from spring blooms as an important, but seasonal, carbon supply. CWC in the Mingulay Reef, as a relative shallow reef, experiences episodic arrival of phytoplankton (Davies et al., 2009; Findlay et al., 2014). Hence, it seems realistic to suggest that *L. pertusa* can rely, at least in some seasons and locations, on phytoplankton as a food source. Stable isotopic analyses conducted on *L. pertusa*, have already shown that zooplankton appear as the main food source but phytoplankton markers were also detected (Carlier et al., 2009). Such a combined diet was observed in the tropical coral *Carijoa riisei* (Duchassaing and Michelotti, 1860), which seems to be a polyphagous species with an overall equitable biomass contribution from phytoplankton and zooplankton (Lira et al., 2009). Previous aquaria experiments conducted in the Antarctica revealed that the gorgonian *Primnoisis antarctica* (Studer, 1878) covers approximately 49% of its daily energy demand by feeding on small plankton (Orejas et al., 2003). The ability of these suspension feeders to capture small cells such as those from phytoplankton may allow them to remain seasonally active for considerably longer periods than previously thought (Orejas et al., 2003). This could be also the case for *L. pertusa*, which is highly tolerant to living on minimal food resources for periods of several months (Larsson et al., 2013).

A slight decrease in POC was detected at 2 cm s^{-1}, but was higher at 5 and 10 cm s^{-1}, but no significant differences were detected among the three current speeds due to high variability. These results are not surprising as release of POM is known from soft and hard corals from warm water reefs (Wild et al., 2004, 2010 and references therein). This supply of organic matter to the surrounding waters frequently occurs through mucus released by corals. The organic matter content in this mucus, makes an important contribution to the ecological functioning of the reefs and acts as a pathway for energy transport and particle entrapment (Wild et al., 2004). It may also constitute an important interaction element between fauna and microorganisms (Wild et al., 2008). Wild et al., 2008 published the first study analysing these aspects for *L. pertusa*, and their results from aquaria experiments revealed a POC release of 1430 ± 1220 μg C m^{-2} h^{-1}, which was comparable to some species of tropical corals. Considering the values obtained by Wild et al. (2008) and extrapolating the POC release values recorded in these experiments (considering a release of around 9 μg C $polyp^{-1}$ h^{-1} by 5 and 10 cm s^{-1} current speed), to 1 m^2 (assuming a minimum number of 1688 *L. pertusa* polyps per square metre; after Cathalot et al., 2015), in the experiment carried out, values of 15,200 C m^{-2} h^{-1} were achieved, which are two orders of magnitude higher than the values from Wild et al. (2008). These different results can be associated to: 1) the use of different methods to calculate the density, and/or 2) to the stress conditions experimented by the corals in the cylindrical experimental chambers (which are a closed circuit in contrast to the open circuit used by Wild et al., 2008) at the beginning of the experiments, which was frequently associated with a visible and abundant mucus release due to handling. This mucus release by CWC would probably play a similar role in tropical and temperate systems, whereby disturbance triggers mucus release and ultimately enhances the microbial activity (Ritchie, 2006) and acts also as an important antifouling agent (Wild et al., 2008 and references therein).

5. Conclusions

This study demonstrated the influence of flow regimes in the capture of different prey type and sizes by *L. pertusa* from the NE Atlantic, supporting previously observed higher capture rates under low current speeds (<7 cm s^{-1}) (Purser et al., 2010). Temperature was not detected

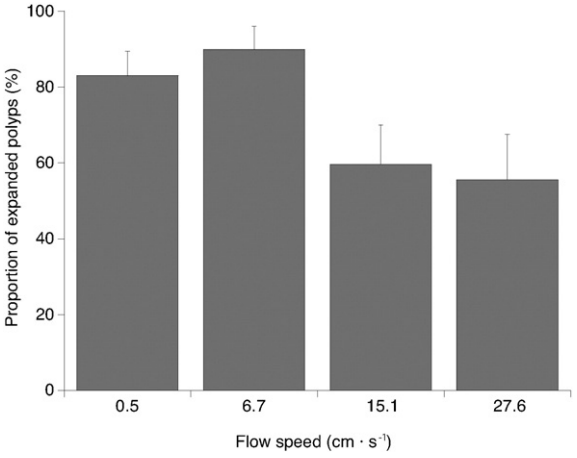

Fig. 5. Colonial response of *Lophelia pertusa* under varying flow speeds. Error bars represent ±1 SE (n = 4 for each treatment).

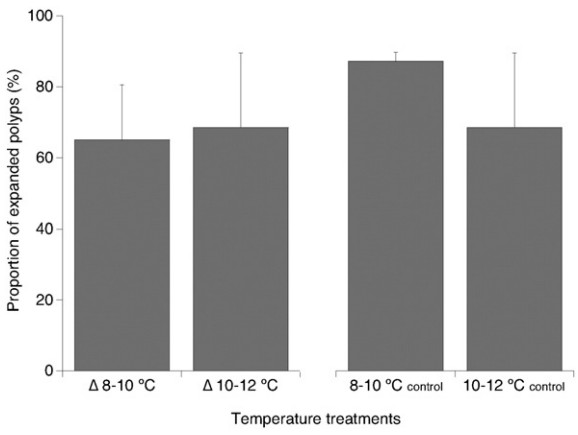

Fig. 6. Colonial response of *Lophelia pertusa* to temperature change (Δ 8–10 °C and Δ 10–12 °C) and independent controls with no temperature change, with observations made at the same duration. Error bars represent ±1 SE (n = 3 for each treatment).

to affect polyp behaviour, suggesting similar expansion responses across a change of 2–4 °C. The polyp behaviour and particle capture (from both zooplankton and phytoplankton), correlated with low flow speeds, also reflects the local environmental conditions of the Mingulay Reef, where a marked tidal regime is characteristic of the area (Davies et al., 2009; Roberts et al., 2009).

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